### *P. dispersa.*

F1 seedlings from the same crosses as those used in the tests with *P. triticina*, and in some instances the very same plants after removal of the rusted first leaves, were tested with the stock culture of rye leaf rust. Attention has been called elsewhere (Waterhouse, 1952) to the absence of clear definition of the physiologic races present, and hence the stock culture was used. Whereas "4" reactions (susceptibility) were shown by the rye variety and "flecks" and "1" reactions by the wheat, the F1 gave "fleck" and "1" reactions.

### *Urocystis* spp.

Grain was inoculated, some with *U. tritici* Kcke. and some with *U. occulta* (Wallr.) Rab., and sown under favourable conditions for infection. "Geeralying" is resistant to both smuts, and the ryes to *U. tritici*. From these crosses no infection was found. In one case where "Federation" was the vulgare parent, infection by *U. tritici* occurred in the F1. In all the tests made no infection by *U. occulta* was found.

### *Tilletia* spp.

The two common species, *T. caries* (D.C.) Tul., and *T. foetida* (Wallr.) Liro, were used in mixed inoculum dusted on the grain. "Geeralying" is susceptible to bunt, and in the case of rye very occasional susceptibility is found. In each sowing that was made, bunted grain of "Federation" was sown as a check because of its extreme susceptibility. In some seasons, when conditions were unfavourable for bunt develop- ment, none developed in "Federation", but in general good infections were found. On numerous occasions bunt (both species) developed in the F1 heads (Plate ii, fig. 7). The bunt "balls" were almost as large as rye grains. This is very striking because of the sterility shown by the F1s. The nature of the stimulus given to "grain" production by the bunt fungus is worthy of full attention. Chlamydospores from the bunted F1 plants were used in the following season to inoculate "Federation" and produced normal infections.

### *Claviceps purpurea.*

A culture derived from ergots on wheat collected at Glen Innes, N.S.W., was used to give a conidial suspension that was sprayed on the plants at flowering time in the Sydney University plot. There were marked seasonal variations in the amount of infection, but this occurred also in both wheat and rye parents. An unexpected happening was the abundant production of ergots in the sterile F1 plants (Plate ii, fig. 5). As in the case of bunt, some remarkable stimulus is given by the fungus to the ovarian tissues of these sterile spikes which leads to the formation of ergots. These are quite as large as those formed in wheat and rye. A weighing of 100 ergots shaken from the F1 plants and 100 shaken from the rye ears showed no significant difference between them. Lightly buried in garden soil and frozen for four months in the ice box of a refrigerator, ergots "germinated" in four weeks and produced normal stromatic heads and perithecia.

In the process of spraying the flowering ears with the conidial suspensions, adjacent rows of *Triticum aegilopoides* Bal. and *T. monococcum* L. were inoculated by chance and produced numerous infected heads (Plate ii, fig. 6). It is usually reported that these species are resistant to ergot attack.

### STRUCTURE OF F1 PLANTS.

In general there was close similarity between the F1 plants derived from the "Geeralying" crosses. All were very tall with foliage resembling that of rye, and produced many heads (Plate i, fig. 1). Beard production was greater from some rye varieties than from others. One unusual head type resembling a durum wheat occurred in one plant of "Geeralying" crossed with "Segales" rye, whereas in all other cases the result was the typical long lax ear (Plate i, fig. 2). No grain was formed in it, so further studies could not be made.

In all cases complete sterility was found in bagged heads. Only very rarely was any grain formed in open-pollinated heads. This makes it more striking that bunt and

ergot should have developed in these ears. Grain that was produced was used in later generation work, the resultant plants showing the widest segregation for morphological and rust resistant characters. Vulgare types producing the sharp "flecks" characteristic of rye have been selected.

Back-crosses with wheat have been made widely, and further promising material produced, with, of course, much sterility in numerous crosses.

Polyembryony has shown up in the rye varieties several times in the form of twinned embryos (Plate ii, fig. 1). One such occurrence was also found in the F1 of "Geeralying" × "Cowra 22" (Plate ii, fig. 2). No differences were evident between the two primary shoots. Each gave the same seedling reaction for rust resistance. At maturity all the heads were of the same nature. Twinning may well have occurred following upon fertilization of a single ovule.

An even more striking abnormality was a triple embryo in the F1 of "Geeralying" × "Petkus Rug". From the grains sown in a pot for inoculation purposes, one weak and two strong shoots were noted close together. Investigation showed that all three emerged from the one grain (Plate ii, fig. 3). The seedling reactions for rust resistance were the same on all three primary leaves. As growth proceeded, secondary tillers developed, being weaker from the shoot already mentioned (Plate ii, fig. 4). At maturity no differences between the heads were apparent, and again there is no evidence that more than one ovule was actually concerned in the happening.

Chlorophyll deficiencies have shown up frequently in the form of albinotic and variegated seedlings of the rye parents; the former have soon died, and in no case has it been possible to establish a variegated strain from them, although this has been done in certain inbred ryes. No chlorophyll deficiency has been found in the F1s.

Branching of the rye ears has occurred. Sometimes this has started about half-way along the length of the spike, at other times there has been a double spike from the base of the rachis (Plate i, fig. 4). From many branched ears in rye varieties progeny have been obtained, but in no case have they shown branching. The branched F1 ears were sterile.

In two of the seasons F1 plants were treated with colchicine, using the agar method. No grain was set in the selfed ears.

### Conclusion.

The relationship between wheat and rye which makes it possible to cross them can be a matter of great importance. In the past the cross has been used in the incorporation of hardiness in wheat varieties, but its potentialities for the transference of disease-resistant characteristics of rye to wheat are very promising. This has a particular application where a highly specialized pathogen like the rust fungus is involved.

As a rule the cross is difficult to make, and the finding of the marked compatibility of "Geeralying" wheat with rye makes the work much easier. As much as 85% grain-setting has been obtained when rye pollen is used, as compared with only 1% when rye was the ovule parent. Sterility in the F1 still poses a serious problem.

Studies of the inheritance of resistance to a number of diseases that attack the parents show that there is a closer relationship of the F1 to the wheat than to the rye parent.

There has been little opportunity of carrying out cytological investigation of the happenings, or of examining the effects of colchicine on the F1, but preliminary work with the latter gave negative results. There is a real need for detailed studies along these lines, as well as for investigation of the stimulus imparted to the gynoecia of sterile F1 plants which leads to the formation of bunt balls when the grain is inoculated with *Tilletia* sp., and of ergots when a suspension of conidia of *Claviceps purpurea* is sprayed upon the stigmas at flowering time.

## *Acknowledgements.*

At many stages valuable help has been given by Drs. I. A. Watson and E. P. Baker. Miss D. E. Shaw has helped consistently in the ergot work. Without the loyal and efficient help of the technical staff the investigations could not have been carried out. To all, grateful thanks are tendered.

Financial assistance is gratefully acknowledged from the Commonwealth Research Grant, The Commonwealth Bank of Australia, and the Rural Bank of N.S.W.

### *References.*

LEIN. A., 1943.—Die genetische Grundlage der Kreuzbarkeit zwischen Weizen und Roggen. *Z. indukt. Abstamm. -u. Vererb Lehre,* 81 : 28-59.

————, 1943.—Die Wirksamkeit von Kreuzbarkeitsgenen des Weizens in Kreuzungen von Roggen ♀ mit Weizen ♂. *Zuchter,* 15, 1-3.

McMILLAN, J. R. A., 1933.—Varieties of wheat in Australia. *C.S.I.R. Bulletin,* 72, pp. 28.

WATERHOUSE, W. L., 1930.—Australian Rust Studies. III. Initial results of breeding for rust resistance. PROC. LINN. SOC. N.S.W., 55 : 596-636.

————, 1939.—A note on crossing wheat and rye. *Aust. Jour. Sci.,* 2 : 63.

————, 1952.—Australian Rust Studies. IX. Physiologic race determinations and surveys of cereal rusts. PROC. LINN. SOC. N.S.W., 77 : 209-258.

## EXPLANATION OF PLATES.

### Plate i.

1. General view of "Geeralying" × rye F1 plants at flowering time, showing abundant ear production. Many of them are bagged to ensure self-pollination.

2. Typical spikes of "Geeralying" × rye F1 plants showing the long lax structure. × ½.

3. Unusual spike of "Geeralying" × "Segales" rye, showing compact structure resembling a durum wheat. × ⅗.

4. Branched spike of "Geeralying" × "Slav" rye F1 plant. × ½.

### Plate ii.

1. Double embryo in "Star No. 2", showing two plumules arising from the one grain. Natural size.

2. Double embryo in F1 of "Geeralying" × "Cowra 22", showing emergence of two plumules from the one coleoptile. Natural size.

3. Triple embryo in F1 of "Geeralying" × "Petkus Rug" rye, showing one weak and two strong plumules arising from the one grain. Natural size.

4. View of the same triple embryo F1 at a later stage of growth, still showing one shoot weaker than the others. × ½.

5. Four spikes of "Geeralying" × rye F1 (to the left) and one of rye (to the right), showing ergot formation. × ⅗.

6. Spikes of *Triticum aegilopoides,* showing formation of ergots. × ⅗.

7. Top group, grains of "Geeralying" wheat; bottom group, grains of open-pollinated rye; and middle group, bunt balls produced in bunted grain of "Geeralying" × rye F1 spikes.

# GENETIC CONTROL IN EUCALYPTUS DISTRIBUTION.

By L. D. Pryor.

(Thirteen Text-figures.)

[Read 25th March, 1953.]

*Synopsis.*

It is deduced that interbreeding *Eucalyptus* species occupy distinctly different ecological situations and that species which grow extensively together are reproductively isolated. Hybrids giving rise to hybrid swarms occurred at the junction of species-areas before settlement. The extensive spread of hybrid swarms is considered to have followed settlement.

### Introduction.

Most *Eucalyptus* forests have two prominent features. The first is the sensitivity of many species to habitat changes which generally results, in any one area, in the presence of a considerable number of species each occupying somewhat different ecological situations. The second is that at the same time, and in a contrary way, there is usually more than one species available to occupy a given ecological situation, so that two or more species are frequently combined as dominants in a single stand.

An examination of these features in some of the *Eucalyptus* communities on the Southern Tablelands of New South Wales in the light of genetic relationships of the species, brings out some striking facts which may be summarized in two statements, viz., (1) interbreeding *Eucalyptus* species occupy distinctly different ecological situations; (2) many reproductively isolated *Eucalyptus* species occur together in pairs which are ecologically co-extensive for major portions of their range, though usually separated at their extremes.

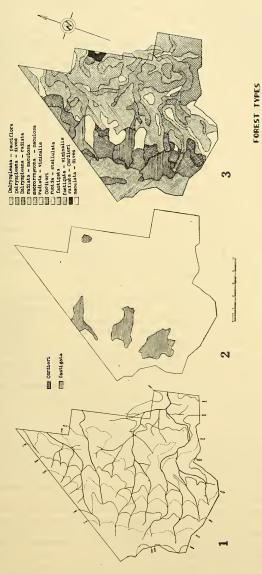### Areas of Detailed Study.

#### Blue Range.

This may be illustrated first by considering an area at Blue Range, Australian Capital Territory, on which the forest types were mapped in detail for another purpose in 1937. The area shows considerable habitat variation with some 2,000 ft. difference in elevation and also with marked differences in aspect (Text-fig. 1). The species present are *E. maculosa*,* *E. Dalrympleana*, *E. viminalis*, *E. rubida* and *E. Cordieri*, belonging to the group Macrantherae of the genus; and *E. pauciflora*, *E. fastigata*, *E. Robertsoni*, *E. dives*, *E. macrorrhyncha* and *E. stellulata*, which belong to the group Renantherae.

Extensive field examination and some manipulated cross pollinations have failed to disclose or produce any hybrids between these two groups of species, but there is evidence that hybridizing can and does occur between most of the species within the two groups. The extent to which this has been detected and confirmed is shown in Table 1.

It will be noticed from Text-figure 2 that, if the area covered by all species in the Macrantherae group taken together is set out and that covered by the Renantherae group is similarly marked, apart from the area occupied by a pure stand of *E. fastigata* and that occupied by a pure stand of *E. Cordieri*, the whole is covered completely at the same time by each group of species. On the other hand (see Text-fig. 3) it will be noticed that there is no area which is occupied by any two species from the one group, Macrantherae or Renantherae.

The area was mapped to show the distribution of the dominant trees, most of which have been living probably since before settlement of the region (about 120 years). Saplings or youthful trees were disregarded in classifying the stands. It is important

* Nomenclature throughout according to Blakely, "A Key to the Eucalypts" (1934).

FOREST TYPES

Dalrympleana – pauciflora
Dalrympleana – dives
Dalrympleana – radiata
radiata – maculosa
macrorrhyncha – maculosa
radiata – viminalis
Cordieri
rubida – stellulata
fastigata
fastigata – viminalis
radiata – Cordieri
maculata – dives

Cordieri
fastigata

3

2

1

Text-figures 1-3.

to note this basis of mapping, as the distribution of species in the pre-settlement period follows a more precisely determined pattern and corresponds more closely with habitat than is the case with the communities regenerated following much increased burning, ringbarking and felling after settlement.

The actual combinations of the two species belonging one to each group which occur at any point are affected by the habitat range of either species. The limit for one may be exceeded at a point still within the zone for successful growth of the other species with which it has been associated, and the combination may therefore change only in one species. This is illustrated in Text-figure 3, where it is seen that *E. Dalrympleana* combines with *E. dives* over a portion of the range of each species, but *E. dives* is able to descend to much lower altitudes than *E. Dalrympleana* and is then commonly combined with *E. maculosa*. This indicates that where two non-interbreeding species can compete for the essentials of life they can grow successfully together. A pure stand no doubt results when the conditions either exceed that possible for all other species in the area, e.g., the *E. Cordieri* pure stand, or otherwise are so favourable to one species that it eliminates the others by competition. This is perhaps the case in the *E. fastigata* pure stands, but in passing it is to be remembered there is a likelihood that pure stands such as *E. fastigata* and other related species, such as *E. gigantea*, are favoured in some circumstances by firing, which, while much less frequent in pre-settlement days, may nevertheless have been a permanent feature of the habitat and, in contrast with the greater frequency following settlement, may have, at the lower pre-settlement frequency, favoured the regeneration of some of these species. Fire may not have been the only cause of such changes; severe storms at occasional intervals may have had the same effect. In this case, therefore, the pure stand of *E. fastigata* may not be a simple elimination of other species by competition, but may be partly conditioned by the regeneration period and, if fire and other possible causes were eliminated, it may in time pass over in many cases to a mixed stand, which in this case would be *E. viminalis–E. fastigata*.

The mapping of Blue Range was designed to express in a broad way the distribution of the vegetation types or associations, and does not fully represent the position with regard to distribution of the species, as the boundaries of the various types are shown as a line on the plan. The types had been decided in advance by inspection of the area. The whole area was mapped according to one or other of the predetermined types. This is an over-simplifiaction as, in fact, the boundary between types is really a zone where the adjoining species are mixed. The extent of the mixed zone depends on several factors, but is generally quite small in relation to the total distribution of either species. For example, in the case of *E. dives* and *E. pauciflora*, the mixed zone occupied not more than one-fiftieth of the altitudinal range of *E. dives* and a still smaller percentage of the altitudinal range of *E. pauciflora*.

### Pierce's Creek.

The nature of the boundaries between species is displayed more clearly at Pierce's Creek, A.C.T., where it is more complicated and has more varied kinds of boundaries. It was selected for mapping for this reason and the method of mapping was changed to display particularly these features.

The whole area was covered by a strip survey and each rectangular piece of ground two chains wide by two and a half chains long over the whole area, was assessed objectively, the species on each parcel of ground simply being recorded in three classes: (1) Dominant: large trees, probably mostly living at the time of settlement; (2) Subdominant: middle-aged trees, somewhat smaller and generally younger than the dominants; and (3) Dominated: seedling coppice and suppressed saplings generally up to about thirty years of age.

This differs from the method of mapping used at Blue Range where, as mentioned above, the combinations of species to be mapped as types were pre-determined by inspection.

In the case of Pierce's Creek there was no pre-determination of types. The species were mapped almost to individual trees, as they actually occurred, and a more precise picture could only be obtained by mapping individual trees.

The species present are: Macrantherae: *E. rubida, E. Stuartiana, E. maculosa*; Renantherae: *E. dives, E. pauciflora, E. Robertsoni, E. macrorrhyncha, E. Rossii*.

As with the groups of species mentioned before at Blue Range their interbreeding position is similar, and is indicated in Table 1.

TABLE 1.

*Renantherae.*

|  | pauciflora | fastigata | Robertsoni | dives | macrorrhyncha | stellulata | Rossii |
|---|---|---|---|---|---|---|---|
| pauciflora |  | xx | xx | xx | x | — | xx |
| fastigata |  |  | xx | x | — | — | — |
| Robertsoni |  |  |  | x | x | xx | xx |
| dives |  |  |  |  | x | — | xx |
| macrorrhyncha |  |  |  |  |  | xx | xx |
| stellulata |  |  |  |  |  |  | — |
| Rossii |  |  |  |  |  |  | — |

*Macrantherae.*

|  | maculosa | Dalrympleana | viminalis | rubida | Cordieri | Stuartiana |
|---|---|---|---|---|---|---|
| maculosa |  | — | x | xx | xx | x |
| Dalrympleana |  |  | xx | — | — | — |
| viminalis |  |  |  | xx | xx | xx |
| rubida |  |  |  |  | xx | x |
| Cordieri |  |  |  |  |  | — |
| Stuartiana |  |  |  |  |  | — |

x = Hybrid determined on morphological evidence.
xx = Hybrid determined on evidence of segregation in a progeny test.

The area displays as a whole features in conformity with the two generalities mentioned at the outset.

The most striking exception is the apparent overlap in the interbreeding species *E. rubida* (Text-fig. 4) and *E. Stuartiana* (Text-fig. 5). The explanation here, however, is simple. The distribution of *E. rubida* in this area is mainly due to the presence of soil which is periodically swampy, and in most cases is represented by narrow flats along drainage channels, and is frequently associated with an understorey of *Leptospermum juniperinum*. This habitat is very sharply cut off from the surrounding areas and is a narrow strip of accumulated soil in contrast with the soil of most of the area which is developed *in situ*. If the *E. rubida* distribution is compared with *Leptospermum* (Text-fig. 6) it will be seen that there is close correspondence. The mixing with *E. Stuartiana* is conditioned by the habitat and is an expression of the mosaic of two distinct habitats. On well-drained soils *E. Stuartiana* and *E. rubida* are not co-dominants in mixed stands. In this particular area the remaining species belonging to the Macrantherae, *E. maculosa* (Text-fig. 7) is almost completely separated from *E. Stuartiana* as it occupies here soils derived from sedimentary rock, while *E. Stuartiana* is mainly on soils derived from granite. In the group of species belonging to the Renantherae it will be seen that all pairs of species, with one exception, are almost entirely separated in their distribution. The exception is *E. dives* and *E. macrorrhyncha*,